

MILLEROCAULIS RICHMONDII SP. NOV., AN OSMUNDACEOUS FERN FROM MESOZOIC STRATA NEAR LITTLE SWANPORT, TASMANIA, AUSTRALIA

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(with two text-figures, one table, and three plates)

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A permineralised rhizome from Mesozoic strata south of Little Swanport, Tasmania, represents a new species of *Millerocaulis* (*M. richmondii*). Its stem is 6 × 7 mm across and is surrounded by adhering leaf bases with each having a stipular expansion typical of the Osmundaceae. The xylem of the ectophloic siphonostele comprising this stem is dissected by leaf gaps and consists of 14 xylem strands in its cylinder. Twenty leaf traces occur in a transverse section of its cortices. The xylem of its leaf traces and petiolar vascular strands is generally curved adaxially with a single protoxylem cluster being median on the trace. This protoxylem cluster bifurcates into two protoxylem groups immediately after leaving the stem and upon entering the petiole. The sclerotic ring of the petiole base is uniform in width and cell-wall thickness. A mass of sclerenchyma present in the adaxial concavity of the petiolar vascular strand expands at higher levels of the petiole until it fills the concavity of the strand and becomes immediately adjacent to the sclerotic ring. A large, round cellular mass of sclerenchyma occurs in the stipular expansions midway between their sclerotic rings and their tips. *Millerocaulis richmondii* is an additional species in the family Osmundaceae which was very abundant in Tasmania during mid-Mesozoic time.

Key Words: Osmundaceae, *Millerocaulis*, Little Swanport, Tasmania, Mesozoic.

INTRODUCTION

Osmundaceae is significant among fern families due to its extensive fossil record, both as leaf compressions and petrified axes and rhizomes. The latter are characterised by having stems with adhering leaf bases and attached adventitious roots (Miller 1967, 1971). The family was particularly important in floras of mid-Mesozoic age in Tasmania (Hill *et al.* 1989, Tidwell 1987, Tidwell & Jones 1987, Tidwell *et al.* 1987, 1991).

One genus of petrified rhizomes in this family is *Millerocaulis* (Tidwell 1986), which has been reported previously from the Triassic through the Lower Cretaceous in Argentina (Archangelsky & De La Sota 1962, 1963), South Africa (Seward 1907), New Zealand and Australia (Gould 1981, Kidston & Gwynne-Vaughan 1907, Tidwell *et al.* 1991, Stopes 1921), Antarctica (Schopf 1978), India (Gupta 1970, Mittre 1955, Sharma 1973, Sharma *et al.* 1979), Peoples Republic of China (Wang 1983), and USA (Tidwell & Rushforth 1970). Species of this genus reported from Tasmania (Tidwell *et al.* 1991) are *M. johnstonii*, *M. spinksii*, *M. websterii*, *M. broganii*, and *M. swanensis*, all from three sites along the eastern coast, and *M. wrightii* from the Lune River locality.

The present report describes a new species of *Millerocaulis* based on a single specimen of silicified rhizome from mid-Mesozoic of Tasmania. This is the third, but the first new, species, reported from localities near Little Swanport. The two species reported earlier from this area are *M. johnstonii* and *M. broganii* (Tidwell *et al.* 1991) with the latter species being collected from the same locality as the specimen upon which this report is based.

MATERIALS AND METHODS

The new species is based upon one black, permineralised specimen from gravels in a small area to the west of Mitchelmores Creek, which lies east of the River Road southwest of Little Swanport (g.c. 42° 20' 45" S, 147° 53' 48" E and UGR 55G EP735113: *Little Swanport* 1:100 000 sheet 8413). The study of the specimen was based mainly on thin sections viewed through a transmitted light microscope. Part of the specimen was also examined under reflected light after being etched with hydrofluoric acid. The age of the locality, other than mid-Mesozoic, remains uncertain.

The specimen is deposited in the Tasmanian Museum and Art Gallery, Hobart, Tasmania.

SYSTEMATIC PALAEOBOTANY

Osmundaceae

Millerocaulis richmondii sp. nov.
(pls 1–3, figs 1, 2)

Diagnosis

Stem rhizomatous, 6 × 7 mm across, surrounded by a mantle of closely adhering stipulated leaf bases; stele ectophloic siphonostele; xylem cylinder dissected, consisting of 14 xylem strands (five strands by Hewitson's [1962] method); pith parenchymatous, 1 mm across; three leaf gaps high and wide, formed opposite departing trace; phloem and external endodermis continuous; inner cortex parenchymatous, homogeneous, 0.75–1.25 mm wide; outer cortex, 1.5–3 mm across; 20 leaf traces per transverse section of cortices; leaf trace C-shaped, single, medial, adaxial protoxylem cluster bifurcating upon initially entering petiole; petiole base stipular; sclerotic ring homogeneous; expanded sclerotic mass in

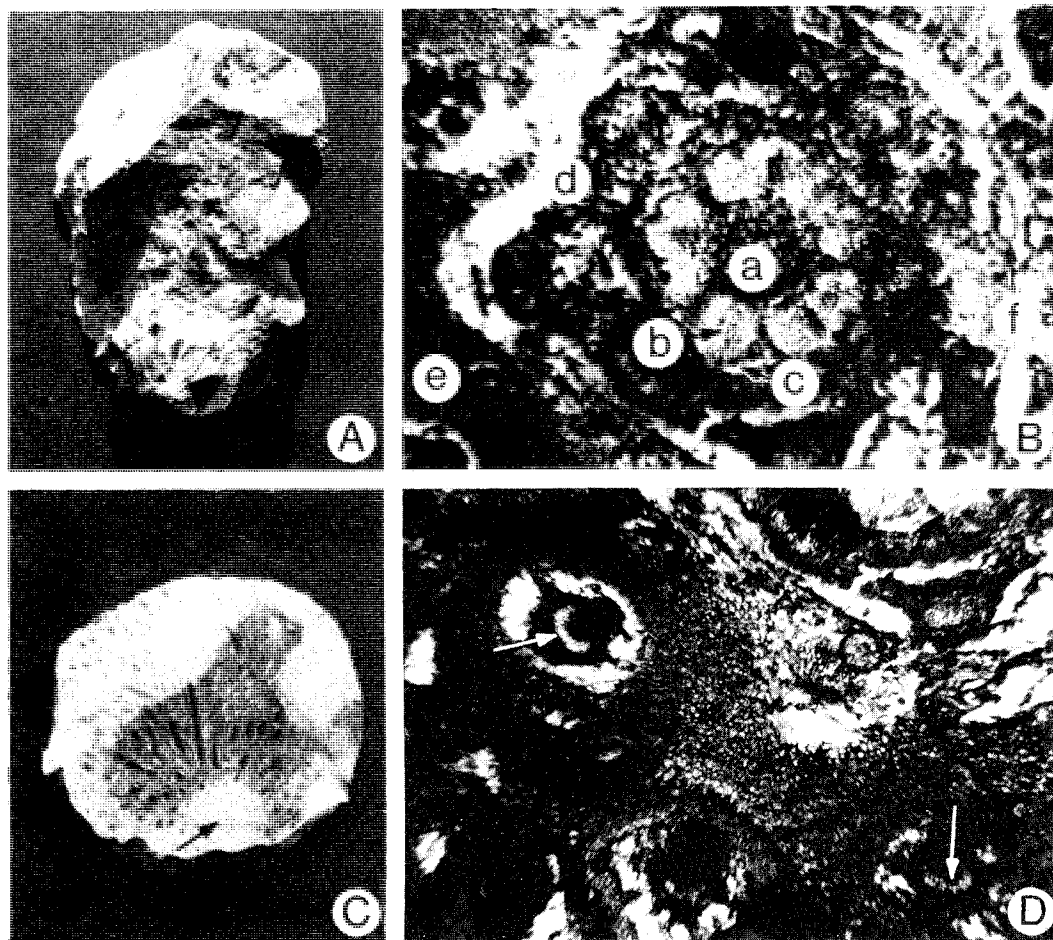


PLATE 1

Millerocaulis richmondii sp. nov. (A) Side view of holotype Z2334, $\times 1$. (B) Transverse section of the stem. Note the pith (a), xylem (b), phloem and endodermis (c), inner cortex (d), and leaf traces (f), $\times 23$. (C) Top view of holotype. Note the smallness of the stem (arrow) surrounded by petioles, $\times 1$. (D) Transverse section illustrating the sclerenchymatous outer cortex containing leaf traces (arrows), $\times 23$.

concavity of petiolar vascular strand, filling concavity distally and connecting with sclerotic ring; single large, round cellular mass in each stipular expansion; roots diverging two per leaf trace, stele exarch.

Repository

Tasmanian Museum and Art Gallery Z2334 (holotype); Hobart, Tasmania.

Etymology

The specific epithet honours Mr John Richmond of South Hobart, Tasmania, for donating the specimen.

Locality

Mitchelmores Creek, south of Little Swanport, Tasmania.

Age

Uncertain, in Holocene gravel derived from older source rock.

Description

The stem of *Millerocaulis richmondii* is small, 6×7 mm across, with a stele having an external diameter of 2 mm and a pith 1 mm across (pl. 1 A–C, fig. 1). Thin-walled parenchyma

cells, $20\text{--}65\text{ }\mu\text{m}$ across, comprise the pith. Smaller parenchyma cells arranged in a single layer of the xylem sheath enclose the pith, extend into the leaf gaps and separate the phloem from the xylem. Thin-walled cells of the leaf gaps are generally uniform in shape and size, becoming larger towards the outside of the xylem cylinder.

The xylem cylinder is dissected and is composed of 14 oval xylem strands that are $8\text{--}10$ metaxylem tracheids in radial width. These strands appear as single strands or horseshoe shaped, with their open ends towards the pith, during trace formation and are composed of scalariform metaxylem tracheids measuring $20\text{--}40\text{ }\mu\text{m}$ wide by $150\text{ }\mu\text{m}$ long. Protoxylem elements are $10\text{--}15\text{ }\mu\text{m}$ across, and no xylem parenchyma is present.

The divergence of the leaf trace from the stele begins with a small amount of parenchyma being inserted between two fused xylem strands, and a protoxylem strand also occurs at this point. This parenchyma develops centripetally, ultimately connecting with the pith and, thus, splitting the strands. The U-shaped part of these strands separates to form the trace, with one side diverging before the other; eventually the other side of the trace breaks away and the characteristic C-shape leaf trace results (pl. 2A). A single protoxylem cluster remains endarch on the inner face of the

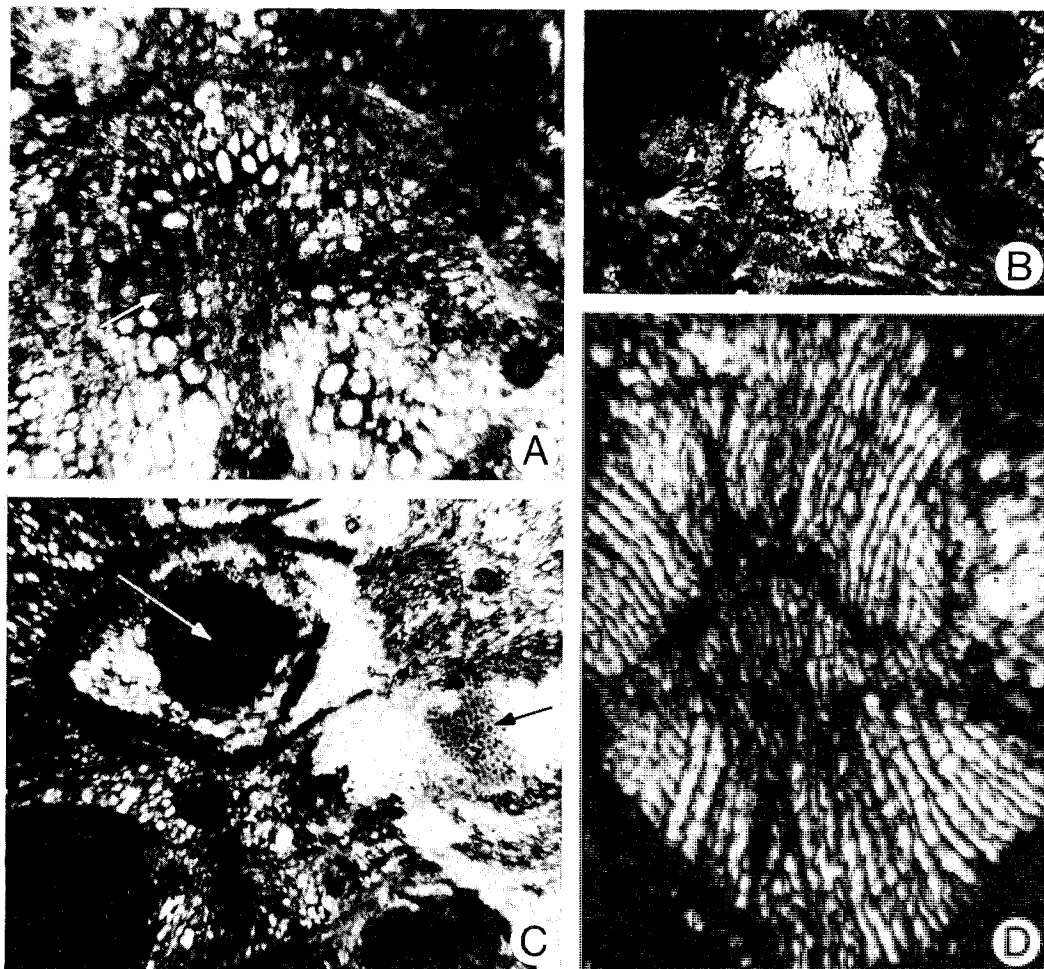


PLATE 2

Millerocaulis richmondii sp. nov. (A) Longitudinal view of leaf trace departing xylem. Note the scalariform pittings (arrow) on the tracheid walls, $\times 75$. (B) Transverse section of a coniferous root that occurred among the petiole bases, $\times 25$. (C) Closeup of a transverse section of petioles with stipular wings attached. Note the sclerenchyma (arrows) in the adaxial concavity of the vascular strands, $\times 25$. (D) Closeup of the root (B). Note tracheids in radial rows, $\times 75$.

curved trace until it bifurcates immediately outside of the stem.

Phloem, 1–3 cells wide, occurs external to the xylem sheath (pl. 1B). The phloem cells are oblong in transverse shape and measure 7×15 – $20 \mu\text{m}$ across. Whether this shape is natural or due to preservation cannot be determined. The phloem is V-shaped at the leaf gaps, with the apex of the V projecting into the gap. Internal phloem is absent. A layer of thin-walled, oblong cells, with each cell being $75 \times 1.25 \mu\text{m}$ across, is interpreted as the endodermis. This tissue occurs around the stele and outlines the leaf traces as they pass through the inner cortex.

Thin-walled parenchyma cells, 25 – $50 \mu\text{m}$ in diameter, lying outside of the endodermis, comprise the inner cortex (pl. 1B, D). No sclerenchyma appears to be present. In this tissue of about 0.75 – 1.25 mm in thickness, 13 leaf traces can be observed. Outer cortex in this species is a sclerenchymatous tissue of thick-walled cells, 35 – $55 \mu\text{m}$ across, and contains seven leaf traces (pl. 1D). This tissue is 1.5 – 3 mm thick, with its actual width difficult to define because of emerging leaf traces.

Passing from the stele towards the periphery of the stem,

the leaf trace begins somewhat flattened near the stele in the inner cortex, becoming strongly curved towards the outside of this tissue, and remaining this shape throughout the outer cortex (pl. 1D).

The xylem in the emerging traces is generally thin, consisting of 2–3 tracheids in width near their middles, and upwards of 5 tracheids at their tips. The phloem is abaxial to the xylem and the endodermis is external to the phloem in these vascular strands. A sclerotic ring surrounds the trace as it leaves the outer cortex. Cells constituting this ring are uniform in size and wall thickness.

A cluster of sclerotic cells occurs in the adaxial concavity of the petiolar vascular strand in the outer cortex (pls 2C, 3A–D). At the base of the petiole, the cluster is small, round, and placed in the middle of the inner cortex of the petiole (fig. 2). Distally it becomes broader and then flattened against the vascular strand (pl. 2B). At a higher level of the petiole, the cluster expands adaxially until it ultimately becomes part of the sclerotic ring (fig. 2). It also widens abaxially, filling the concavity of a broadly flattened strand. This expanded sclerotic cluster starts somewhat triangular in shape, 0.5 mm across with rounded angles, and higher up

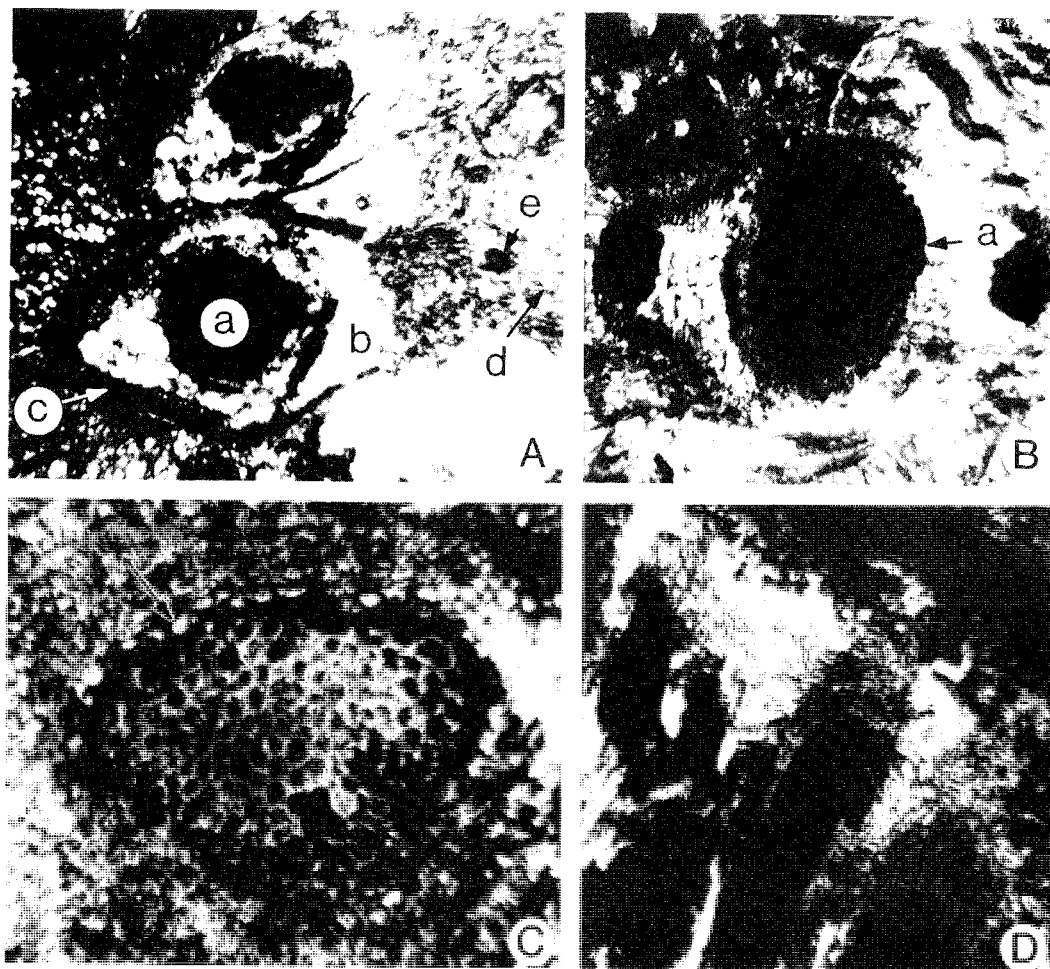


PLATE 3

Millerocaulis richmondii sp. nov. (A & B) Close-ups of transverse sections of petioles with stipular wings attached. Note the sclerenchyma in the adaxial concavity of the petiolar strand (a), inner cortex of the petiole (b), sclerotic ring (c), the stipular wing (d), and the mass of sclerenchyma in the wing (e), $\times 25$. (C) Enlargement of the sclerenchyma in the adaxial concavity of the petiolar vascular strand (arrow), $\times 25$. (D) Longitudinal view of several petioles. The long black objects are the sclerenchyma in the petiolar strands and the wavy cells compose the stipular wings, $\times 75$.

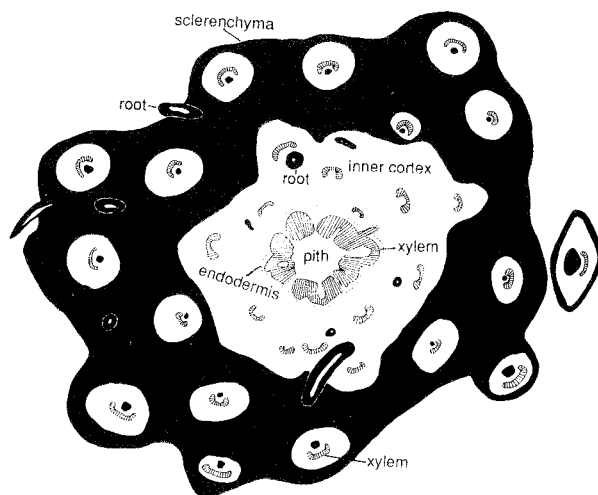


FIG. 1—*Millerocaulis richmondii* sp. nov. Transverse section of the stem with one petiole. $\times 12.5$.

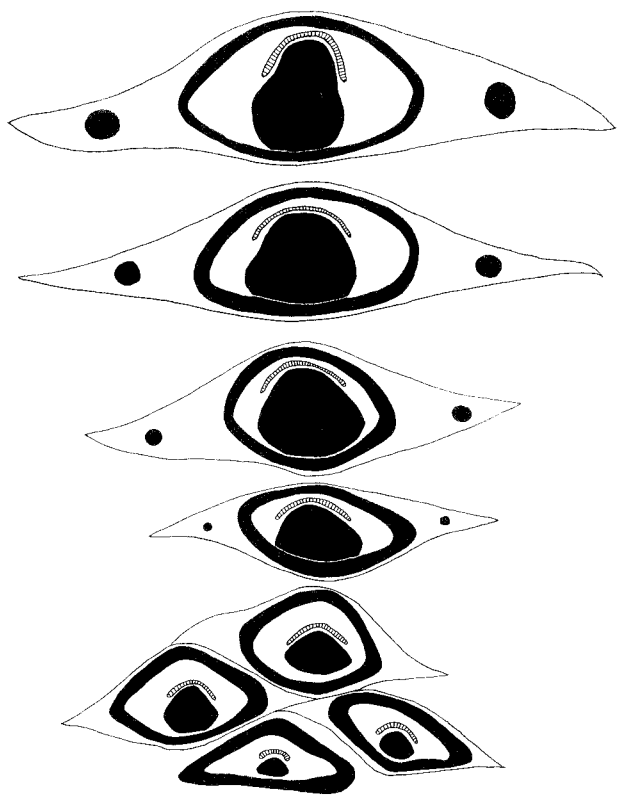


FIG. 2 — *Millerocaulis richmondii* sp. nov. Transverse sections of petioles with stipular wings attached illustrating changes that occur at progressively higher levels of the petioles. Note how the sclerenchyma in the adaxial concavity of the vascular strand and the sclerenchyma mass in the wing enlarges upwards in the petiole. Black = sclerenchyma.

is oblong and 1 mm wide. The parenchyma cells of the inner cortex of the petiole are round, 25–30 μm wide (pl. 3A). No other sclerenchyma is present in the inner cortex of the petioles.

Leaf bases are stipular with the expansions at lower levels being relatively short, but become elongated upwards. They measure 2–3 mm from the sclerotic ring to their tip. The parenchyma cells making up the wing are distorted (pl. 3D) and measure 50–60 μm across. The epidermis of these wings is poorly preserved and can be defined by a black line 2 μm wide. A large, round cellular mass of sclerenchyma, 100–200 μm across, occurs midway between the ring and the tip of the stipular wing (pl. 3A). This mass is small at lower levels, becoming three times as large at higher ones.

Surprisingly, only a small number of roots occur in this specimen. They are exarch and protostelic, and arise from the leaf trace before the traces leave the stele. The xylem of the roots begins round and eventually becomes elliptical. Metaxylem trachery elements in these protosteles are 20–30 μm in diameter and 120 μm long. The phloem, pericycle, endodermis and inner cortex are not preserved. The sclerotic outer cortex consists of thick-walled cells 15 μm across. The epidermis is also not preserved. Most of the roots were sectioned longitudinally in transverse stem sections, suggesting a rhizomatous nature for the stem (Miller 1971).

An unidentifiable root occurs among the petiole bases in the specimen (pl. 2B, D). The root measures 0.75 \times 1 mm

across, with tracheids arranged in radial rows, and appears to be from a conifer, because of its secondary growth and its xylem composition being only tracheids.

COMPARISONS AND DISCUSSION

Millerocaulis richmondii differs most significantly from the other members of *Millerocaulis* in the amount of sclerenchyma in the adaxial concavity of its leaf and petiolar traces. None of the others consistently have the large amount of sclerenchyma that is present in *M. richmondii*. The species closest to having this amount is *M. wadei* (Tidwell & Rushforth 1970) Tidwell from the Upper Jurassic Morrison Formation in eastern and central Utah, USA. Most petioles of the latter species contain sclerenchyma flattened against their vascular strands. In some petioles, however, the masses broaden adaxially, like those in *M. richmondii*, to become part of, or at least be appressed into the sclerotic cylinder surrounding the strand. These large masses of sclerenchyma do not occur in all the petioles of *M. wadei* as they do in *M. richmondii*.

Millerocaulis richmondii is similar to the Tasmanian species *M. spinksii*, *M. broganii*, and *M. johnstonii* in its size and the trace number in its cortices (table 1), but differs from them in possessing a large mass of sclerenchyma in the concavity of its petiolar strand, in lack of sclerenchyma in the wings of *M. spinksii*, the more numerous xylem strands and the heterogeneous pith of *M. broganii*, and the heterogeneous sclerotic ring and sclerenchyma lining the petiole strand in *M. johnstonii* (table 1).

This new species from Tasmania also differs from other species of *Millerocaulis* from the Southern Hemisphere. It is unlike *M. dunlopii* (Kidston & Gwynne-Vaughan 1907) Tidwell and *M. gibbiana* (Kidston & Gwynne-Vaughan 1907) Tidwell, both from Queensland, Australia and New Zealand, in having only one mass in its wings rather than numerous small masses as in *M. dunlopii* and 12 linear ones in *M. gibbiana*. It has a homogeneous sclerotic ring rather than the heterogeneous ring of *M. kidstonii* (Stopes 1921) Tidwell from Queensland. It is also not arborescent like *M. kolbei* (Seward 1907) Tidwell of South Africa. *Millerocaulis patagonica* (Archangelsky & De La Sota 1962) Tidwell and *M. herbstii* (Archangelsky & De La Sota 1963) Tidwell of South America have more numerous masses of sclerenchyma in their wings (10 in *M. patagonica* and 3–5 in *M. herbstii*) as compared to one in *M. richmondii*.

Millerocaulis beardmorensis (Schopf 1978) Tidwell from Antarctica differs by having a mixed pith which does not occur in this Tasmanian species.

Of the seven species described from Tasmania, *M. richmondii* is anatomically intermediate (table 1). Based upon fourteen characters proposed by Miller (1971) for judging whether an osmundaceous form is primitive or advanced, *M. richmondii* has seven that are primitive and six that are advanced, with one being intermediate. The primitive characters in *M. richmondii* are a homogeneous, parenchymatous pith, external endodermis and phloem, parenchymatous inner cortex, protoxylem bifurcating in petiole, a single, albeit large, mass of sclerenchyma in the concavity of its petiolar strands, homogeneous sclerotic ring, and having a single mass of sclerenchyma in each stipular wing. Its advanced characters are a rhizomatous habit, low number of xylem strands and a thin xylem cylinder, thick outer and thinner inner cortex, as well as a

Table 1
Comparison of the *Millerocaulis* species from Tasmania with *M. richmondii*.*

Species/ locality†	Stem size (mm)	Pith (mm)	Xylem cylinder width (mm)	Xylem strand no.	Inner cortex (mm)	Outer cortex (mm)	Trace no.	Scler. in concavity	Scler. in cortex	Scler. ring	Scler. in wing	PX divides	Root origin
<i>M. richmondii</i> Loc. 4	6x7	homog. 1	2 8-10 tr.	14	homog. 0.75-1.25	1.5-3	20	fills oblong	none	homog.	1 mass	petiole	l.tr. n.st.
<i>M. wrightii</i> Lune River	18-20	homog. 4	0.5-1 9-15 tr.	50-55 (21H)	homog. 2-4	3-5	50	2 near trace	none	homog.	1 mass 2-4 linear	petiole	l.tr. n.st.
<i>M. johnstonii</i> Loc. 1,3	10	homog. 0.25	0.5 7-10 tr.	17(6H), 8(3H) branch	homog. 1	3	25	lining	none	heterog.	1 mass	petiole	l.tr. n.st.
<i>M. spinksii</i> Loc. 2	9-12 brnchg	homog. 0.75-1	0.5-1.25 8-14 tr.	27,14(3H) branch	homog. 0.75-1.25	1.5-2	11-18 23 in paratype	none	none	homog.	none	petiole	l.tr. cortex
<i>M. websterii</i> Loc. 2	15-17	homog. 3	1 12-15 tr.	28-29(7H)	homog. 0.5-2	4	56	none	none	homog.	gen. none 1 mass very rare	petiole	l.tr. cortex
<i>M. broganii</i> Loc. 2,4	7-8 brnchg	heterog. 0.5	0.5 8-12 tr.	20-24 (6-8H)	homog. 0.75-1	1-2	28-29	2 near trace	none	homog.	1 mass	inner cortex(?)	l.tr. n.st.
<i>M. swanensis</i> Loc. 2	3-6 brnchg	homog. 0.25	0.25 7-9 tr.	10(3-4H) branch	homog. 0.3-0.5	0.75-1	6-8	2 near trace	none	homog.	1 mass	petiole	l.tr. n.st.

* Modified from Tidwell *et al.* 1991.
† Localities: 1 – A gravel pit north of the Lake Leake Road. 2 – Gravels in a road cutting (road cut) and surrounding area on Coles Bay Road, north of the Swanwick turnoff. 3 – Floodplain of White Hut Creek, Little Swanport. 4 – Gravels on bank of Mitchelmores Creek (for more data see Tidwell *et al.* 1991).
Abbreviations: brnchg = branching, homog. = homogeneous, scler. = sclerenchyma, l.tr. = leaf trace, H = number by Hewitson’s (1962) method, heterog. = heterogenous, PX = protoxylem, n.st. = near stele, tr. = tracheid.

large amount of sclerenchyma in the plant (Wagner 1964), although there is none in the inner cortex of the petiole.

Distribution of sclerenchyma in the leaf bases and stipular wings in species of the Osmundaceae have been considered to be the most dependable anatomical taxonomic characters upon which to base their separation (Hewitson 1962, Miller 1967, 1971). In general, this appears to be true. However, five species (*M. wadei*, *M. johnstonii*, *M. broganii*, *M. swanensis* and *M. richmondii*) all have similar single masses of sclerenchyma in their stipular wings and seven (*M. patagonica*, *M. kidstonii*, *M. dunlopii*, *M. gibbiana*, *M. wrightii*, *M. broganii* and *M. swansensis*) similarly have two adaxial sclerenchyma masses against the tips of their petiolar vascular strands. Thus, these characters may not always be as distinct as originally thought. These species are distinguished by other characters. However, this illustrates how, in general, species in this family should not be distinguished only on one feature, but rather should be separated on a composite of several different ones.

The age of *M. richmondii* and most of the other Tasmanian species of *Millerocaulis* is unknown. At present, there appears to be a good chance they came from the Upper Triassic (Tidwell *et al.* 1991). However, anatomically this group of species appears to be rather advanced to be this age. Since their source is unknown, their actual age and how they fit phylogenetically into the Osmundaceae must await more conclusive stratigraphic evidence.

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